

Cytogeography of the *Adiantum pedatum* Complex (Pteridaceae, Subfamily Adiantoidae)

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A chromosomal survey revealed that Japanese populations of the *Adiantum pedatum* complex (Pteridaceae, subfamily Adiantoidae) include four cytotypes: diploids of $2n = 58$ ($x = 29$) and $2n = 60$ ($x = 30$), and tetraploids of $2n = 118$ and $2n = 120$ ($x = 30$). The few North American plants we analyzed were diploid ($2n = 58$) and triploid ($2n = 87$) ($x = 29$). The two tetraploid cytotypes in Japan and the triploid from Canada are new cytotypes for this complex. In Japan, diploids with $2n = 60$ are widely distributed at all elevations throughout Hokkaido, Honshu and Shikoku. Diploids with $2n = 58$ are known from only two lowland sites in eastern Hokkaido. Tetraploid plants with $2n = 118$ and 120 are rare in the high mountains of central Honshu and a tetraploid plant with $2n = 118$ is known from a lowland site in central Hokkaido. Asian members of the *A. pedatum* complex have a base chromosome numbers of both $x = 29$ and 30 , whereas North American plants are known to have only $x = 29$ as a base number. Since $x = 30$ is considered to be ancestral in *Adiantum*, it is inferred that the $x = 29$ cytotype in the *A. pedatum* complex originated in Asia and plants with this number later migrated to North America. Other possibilities are that plants with $x = 30$ went extinct in North America, or they have yet to be found.

Key words: *Adiantum pedatum*, base chromosome number, cytogeography, cytotype, polyploidy.

The *Adiantum pedatum* L. complex (Pteridaceae, subfamily Adiantoidae) is a typical example of taxa distributed disjunctly in temperate eastern Asia and North America, a distribution pattern known since the late 18th century (Christ 1910, Boufford & Spongberg 1983, Kato & Iwatsuki 1983). The complex shows three remote centers of distribution; eastern Asia, western North America and eastern North America (Hultén 1968, Sugawara 1975, Fomin 1986, Kurata & Nakaike 1987, Lin 1990, Kato 1993, Paris 1993, Khullar 1994). The historical biogeography of the complex remains uncertain. Cytologically, *A. pedatum* includes diploids based on $x = 29$ and 30 in Asia, and a diploid and a

tetraploid based on $x = 29$ in North America (Table 1). Paris *et al.* (1990) made a preliminary systematic study of the complex based on chloroplast DNA variation, cytology, and isozyme electrophoresis, and suggested that there are at least three diploid species, one each in eastern Asia, western North America, and eastern North America. Paris & Windham (1988) and Paris (1991, 1993) reported that the North American complex comprises three distinct species; *Adiantum pedatum* sensu stricto ($2x$) in eastern North America, *A. aleuticum* (Rupr.) Paris ($2x$) in western and rarely in eastern North America, and *A. viridimontanum* Paris ($4x$) restricted to serpentine areas in Vermont, eastern North

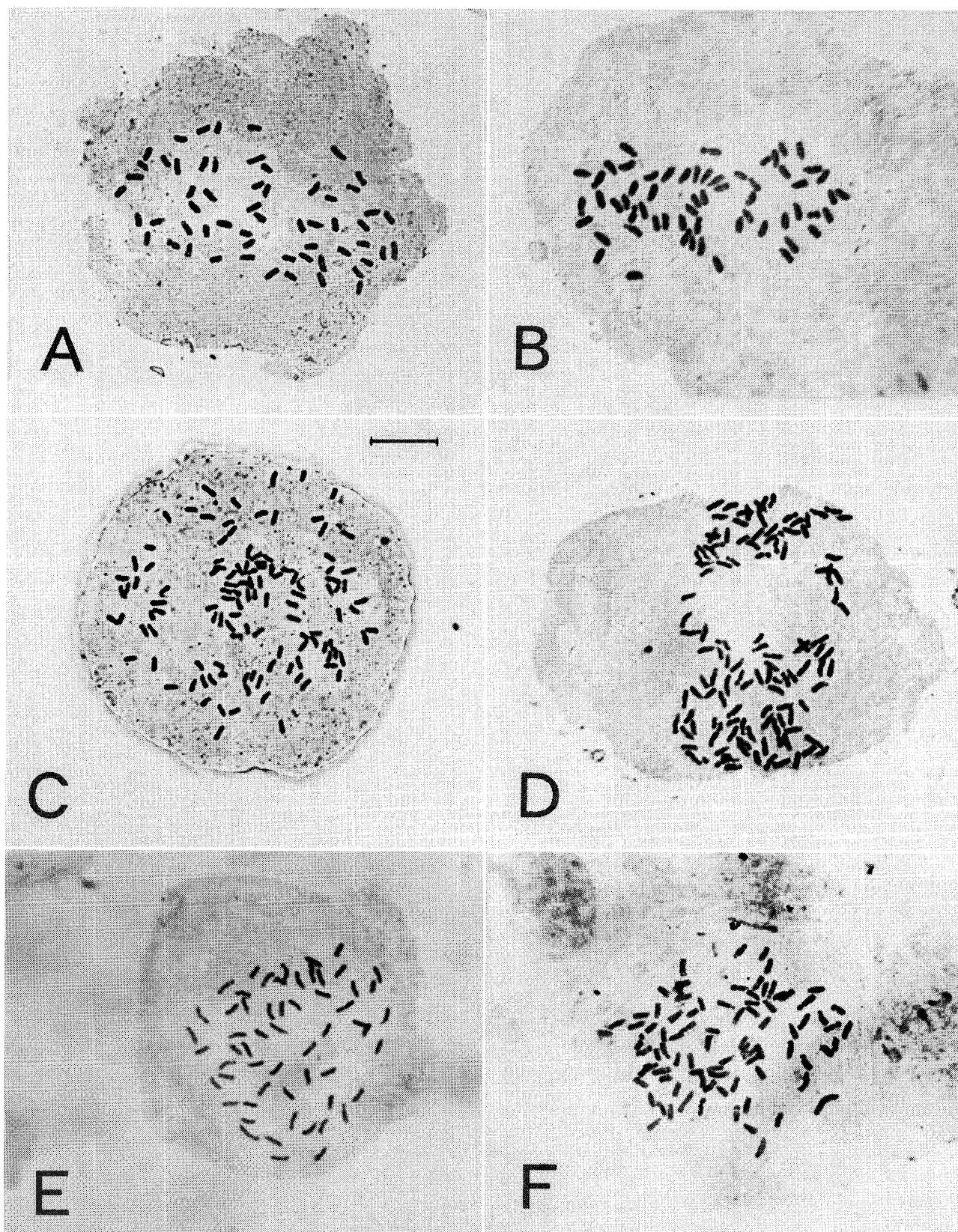


FIG. 1. Somatic chromosomes in the *Adiantum pedatum* complex. For detailed collection data see Table 2. A-D. Japanese plants. A. diploid ($2n = 58$), no. 2155. B. diploid ($2n = 60$), no. 1923. C. tetraploid ($2n = 118$), no. 1666. D. tetraploid ($2n = 120$), no. 1473. E-F. North American plants. E. diploid ($2n = 58$), no. 1823. F. triploid ($2n = 87$), no. 1670. Scale bar = 10 μm .

America. By contrast, the systematics and cytotaxonomy of the Asian entities have not been well investigated, but two base chromosome numbers have been recognized, based on a small number of counts (Table 1). To gain a greater understanding of this complex, we undertook a survey of the chromosomes in the complex, based mainly on plants in Japan.

Materials and Methods

Materials used in the present study were collected from 47 localities (65 individuals) in Japan and three localities (five individuals) in North America (Table 2). For mitotic chromosome observations, root tips were pretreated with a 0.002M solution of 8-hydroxyquinoline for 3–6 hr, fixed in 45% acetic acid for 15 min, macerated in a mixture of 1N HCl and 45% acetic acid (3:1) for 1 min at 60°C, and then squashed in 2% aceto-orcein. Spores were embedded in Eukitt (O. Kindler, Germany), and the equatorial diameter was measured for 20 samples per specimen. Cytological voucher specimens are deposited in the herbarium of the University of Tokyo (TI).

Results and Discussion

Chromosome counts

Chromosome counts obtained in this study are summarized in Table 2. We confirmed four cytotypes in Japanese plants. They are diploids with $2n = 58$ (five plants from two localities), diploids of $2n = 60$ (54 plants from 41 localities), tetraploids with $2n = 118$ (three plants from two localities), and tetraploids with $2n = 120$ (three plants from two localities) (Figs. 1 & 2). In previous studies of Japanese *Adiantum pedatum*, Kurita (1960) and Mitui (1968) recorded $n = 29$ ($2x$, $x = 29$), whereas Mitui (1976), Nakato (in Mitui 1976) and Kawakami (1979, 1981) reported $n = 30$ or $2n = 60$ ($2x$, $x = 30$) (Table 1). From outside Japan, diploids with $x = 29$ were reported from the Sikkim Himalaya and North America, a tetraploid with $x = 29$ from Vermont, eastern U.S.A. (Table 1). The two Japanese tetraploids with $2n = 118$ and $2n = 120$ are newly reported cytotypes for the *A. pedatum* complex. As for the North American plants (= *A. pedatum* sensu stricto), two individuals from Massachusetts and two from Vermont were found to be diploid, with $2n = 58$, which is consistent with previous chromosomal studies from North America (Table 1). One indi-

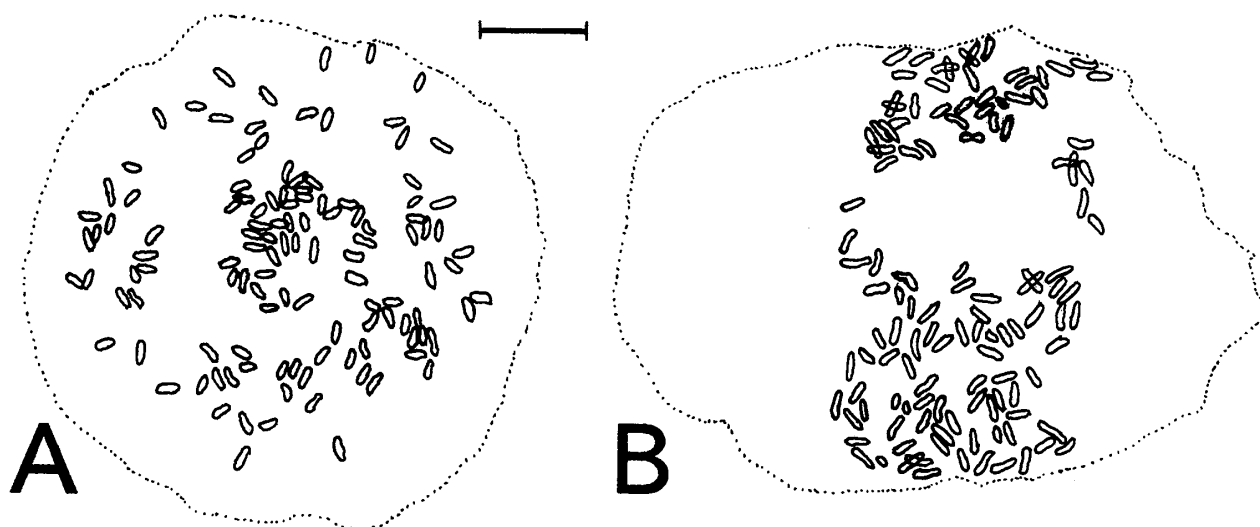


FIG. 2. Explanatory drawings of chromosomes. A. tetraploid ($2n = 118$) of Fig. 1C. B. tetraploid ($2n = 120$) of Fig. 1D. Scale bar = 10 μ m.

vidual from eastern Canada was a triploid, with $2n = 87$, or $x = 29$, and is also a new cytotype in this complex.

Distribution of the four cytotypes in Japan

Figure 3 is a cytogeographic map of the *Adiantum pedatum* complex, based on the present and previously published studies shown in Tables 1 and 2. The imprecise chromosome counts by Mitui ($n = c. 29$, 1975) and Löve & Löve ($2n = c. 58$, 1964) are excluded. Figure 4 shows the altitudinal distribution of the four cytotypes in Japan. Diploids of $2n = 60$ were found at a wide range of elevations, from 20 to 1500 m, in a variety of habitats, such as forest floors and forest edges and openings in broad-leaved deciduous and mixed forests, and also on rocky slopes and stone walls in semi-open places. Diploids with $2n = 58$ were collected on the edges of coniferous and deciduous broad-leaved mixed forests at 20 m and 80 m elevation in Hokkaido. Kurita (1960) reported a diploid of $x = 29$ from Mt. Buko, Saitama Prefecture, which is a limestone region. However, the two localities of the $2n = 58$ diploids in eastern Hokkaido are not calcareous; Abashiri (nos. 2164, 2166) is in a siltstone region, and Kitami (nos. 2155, 2156, 2159) belongs to the Sorachi geologic group consisting of schalstein (wollastonite), basalt lava, chert, mudstone and sandstone (Satoh & Hata 1990).

Tetraploids with $2n = 118$ were found at one locality in central Honshu and one in Hokkaido, while tetraploids with $2n = 120$ were found at two sites in central Honshu. The $2n = 118$ cytotype in Honshu (nos. 1665, 1666) was collected from the forest floor at 1550 m in a sandstone-mudstone area (Yamada & Kato 1991) in the upper zone of a broad-leaved deciduous forest [mainly *Cercidiphyllum japonicum* Sieb. & Zucc. and *Ulmus laciniata* (Trautv.) Mayr] mixed with conifers (*Abies homolepis* Sieb. & Zucc.). The tetraploid with $2n = 118$ (no. 1787) in Hokkaido was found in a thicket along a path in a limestone area (Satoh & Hata

1990) at a relatively low elevation of 240 m.

Tetraploid cytotypes with $2n = 120$ were found in a montane andesite area (Yamada & Kato 1991) at 1480 m (no. 1709), and in an area of intermingled black-shale, schalstein and sandstone (Yamada & Kato 1991) at 1750 m and 1800 m (nos. 1472, 1473), where *Adiantum pedatum* reaches its highest elevation in Japan. Population no. 1709 was in relatively rich soil, 15–20 cm thick, in a deciduous forest (mainly *Cercidiphyllum japonicum* and several species of *Acer*), and population nos. 1472 and 1473 were in the lower zone of a montane coniferous forest (*Abies veitchii* Lindl.). The Japanese tetraploids therefore occur in various geological formations. By contrast, the North American tetraploid *A. viridimontanum* ($2n = 116$, $x = 29$) is restricted to exposed serpentine areas at 200–800 m (Paris & Windham 1988, Paris 1993).

Since the Japanese tetraploid cytotypes are restricted to a much narrower range than the diploids, they seem to be of relatively recent origin as in the case of an American tetraploid (*Adiantum viridimontanum*; Paris & Windham 1988). The tetraploids with $2n = 120$ are likely to have arisen by chromosome doubling of a $2n = 60$ diploid, while the $2n = 118$ tetraploids appear to be either allotetraploid derivatives of a hybrid between the $2n = 58$ and $2n = 60$ diploids, or an aneuploid of the $2n = 120$ tetraploid. The occurrence of the tetraploids ($2n = 118$ and 120) in central Honshu are certainly correlated with severe environments at high elevations. It may be that they originated there. The relationship of the tetraploids with $2n = 118$ on Honshu and Hokkaido is still uncertain. They may have originated independently, because their localities are about 1000 km apart.

External morphology and spore size of Japanese cytotypes

The North American *Adiantum pedatum* sensu stricto ($2x$), *A. aleuticum* ($2x$) and *A. viridimontanum* ($4x$) are discriminated from each other by such

morphological characters as the form of the leaves and pinnule segments, the depth of the segment sinus, the length of the segment stalk and false indusia, rhizome differences, and spore sizes (Paris & Windham 1988, Paris 1991, 1993). When we examined the external morphology of the four

Japanese cytotypes, however, we could not find diagnostic characters to distinguish them. The form of the segments, the size of the segment sinus and the length of segment stalk and false indusia are variable, in particular in the $2n = 60$ diploids; the variation in these characters in the $2n = 60$ diploids

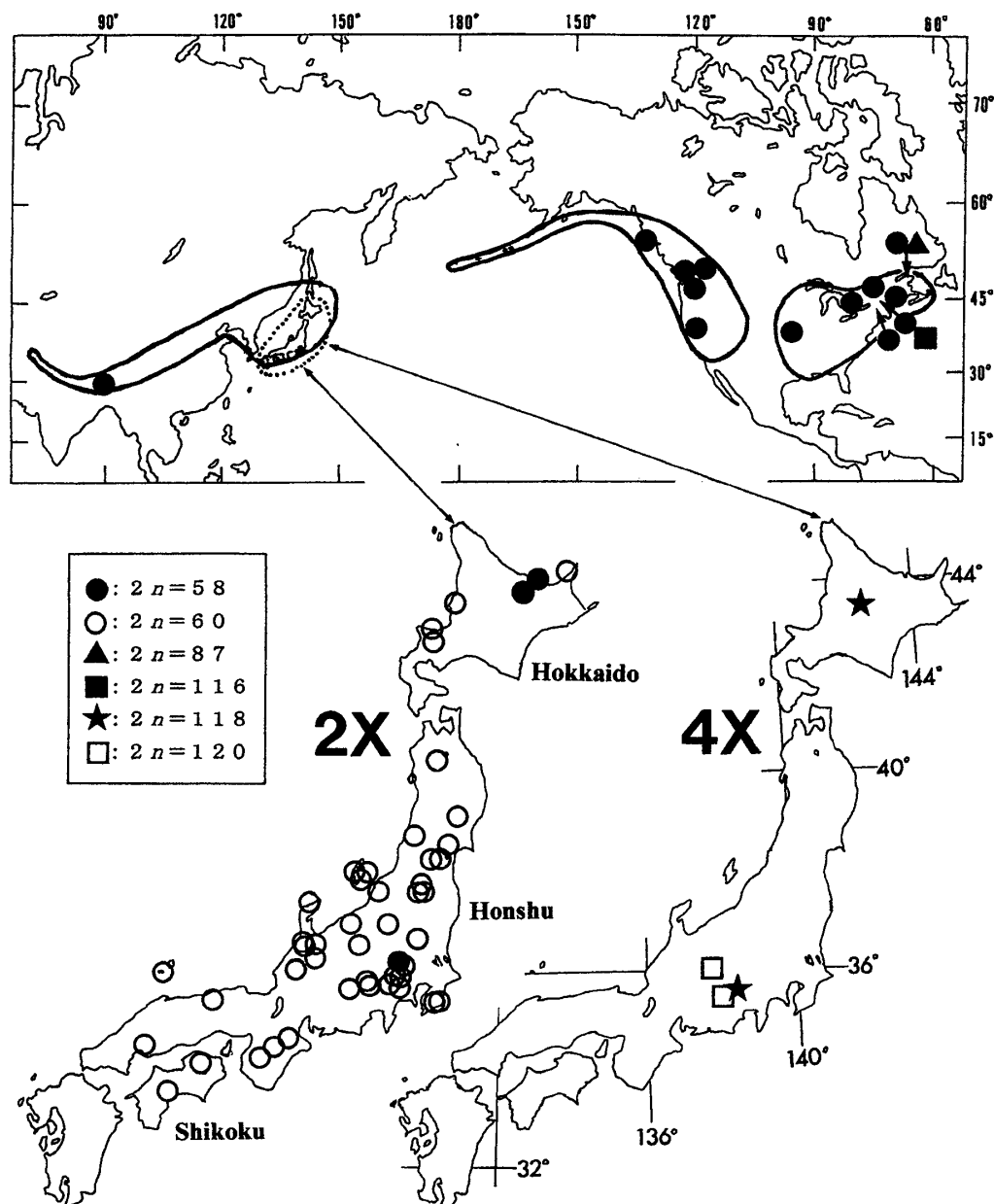


FIG. 3. Distribution of cytotypes of the *Adiantum pedatum* complex. Solid lines indicate distribution ranges. Dotted line corresponds to magnified maps of Japan. Materials cited in Tables 1 and 2 are used.

TABLE 1. Summary of published chromosome numbers in the *Adiantum pedatum* complex.

Locality	Chromosome number		Ploidy	Reference
	n	2n		
EASTERN ASIA				
HIMALAYA				
Sikkim	29	-	2x	Verma in Mehra 1961
JAPAN				
Haboro, Hokkaido Prefecture	c. 29	-	2x	Mitui 1975
Yahiko, Niigata Prefecture	30	-	2x	Mitui 1976
Myokosan, Niigata Prefecture, alt. 1450 m	-	60	2x	Nakato in Mitui 1976
Yoro-keikoku, Chiba Prefecture, alt. 150 m	-	60	2x	Nakato in Mitui 1976
Itsukaichi, Tokyo Prefecture, alt. 550 m	-	60	2x	Nakato in Mitui 1976
Bukosan, Saitama Prefecture	29	-	2x	Kurita 1960
Otsuki, Yamanashi Prefecture, alt. 500 m	-	60	2x	Nakato in Mitui 1976
Eiheiji, Fukui Prefecture, alt. 300 m	-	60	2x	Nakato in Mitui 1976
Hiroshima City, Hiroshima Prefecture	-	60	2x	Kawakami 1979 & 1981
WESTERN NORTH AMERICA				
Graham Isl., Queen Charlotte Isls., Canada	29 ^a	-	2x	Taylor & Mulligan 1968
Big Bend, British Columbia, Canada	-	c. 58 ^a	2x	Löve & Löve 1964
Big Bend, Alberta, Canada	-	58 ^a	2x	Löve & Löve 1976
Vancouver, Canada	29	-	2x	Manton & Sledge 1954
Washington, U.S.A.	29 ^a	-	2x	Wagner in Fabbri 1963
California, U.S.A.	29	-	2x	Wagner 1963
EASTERN NORTH AMERICA				
Mont Albert, Gaspé, Quebec, Canada	29 ^b	-	2x	Cody & Mulligan 1982
Mont Albert, Gaspé, Quebec, Canada	29 ^b	-	2x	Cody 1983
Ile Bizard, Quebec, Canada	-	58	2x	Löve & Löve 1976
Gatineau Park, Quebec, Canada	29	-	2x	Cody & Mulligan 1982
Toronto, Ontario, Canada	29	-	2x	Britton 1953
Exeter Wildflower Gard., Exeter, U.S.A.	29	-	2x	Cody & Mulligan 1982
Belvidere Mt., Vermont, U.S.A.	58 ^c	116	4x	Paris & Windham 1988
Breidenthal Biol. Reserve, Baldwin City, Kansas, U.S.A.	29	-	2x	Rabe & Haufler 1992
Breidenthal Biol. Reserve, Baldwin City, Kansas, U.S.A.	54I+2II ^d	-	2x	Rabe & Haufler 1992
Breidenthal Biol. Reserve, Baldwin City, Kansas, U.S.A.	-	116 ^e	4x	Rabe & Haufler 1992
ORIGIN UNKNOWN or DOUBTFUL				
Origin unknown (cult. in Tokyo Univ. of Education)	29	-	2x	Mitui 1968
Origin unknown (horticultural strain)	29 ^f	-	2x	Wagner 1963
Origin unknown (cult. in Niles, Michigan, U.S.A.)	29 ^g	-	2x	Wagner & Boydston 1978
Origin unknown (cult. in Univ. of Kansas, U.S.A.)	29	58	2x	Paris & Windham 1988
Costa Rica ^h	22 ^h	-	2x	Gòmez 1971

a: As *Adiantum pedatum* var. (or ssp.) *aleuticum*. b: As *A. pedatum* ssp. *calderi*. c: $n = 56\text{II}+1\text{IV}$, $n = 57\text{II}+2\text{I}$ and $n = 55\text{II}+2\text{I}+1\text{IV}$ were also recorded. d: Chromosome count from diploid mutant. e: Autotetraploid obtained by selfing from diploid mutant; 58 chromosomes were also recorded at mitosis in the gametophyte. f: As *A. pedatum* f. *miniature*. g: As *A. pedatum* var. *subpumilum*. h: Doubtful for both locality and chromosome number.

TABLE 2. Summary of chromosome counts in the *Adiantum pedatum* complex obtained in the present study.

Locality (Number of individuals examined in parentheses)	Chromosome number (2n)	Ploidy	Voucher ^a
JAPAN			
Futatsuiwa, Abashiri, Hokkaido Prefecture, alt. 20 m (2)	58	2x	2164, 2166 ^b
Kitakami, Kitami, Hokkaido Prefecture, alt. 80 m (3)	58	2x	2155 ^b , 2156 ^b , 2159
Iwaobetu, Syari-cho, Hokkaido Prefecture, alt. 40 m (1)	60	2x	2162 ^b
Uryu-cho, Hokkaido Prefecture, alt. 200 m (1)	60	2x	1793 ^b
Jozankei, Sapporo, Hokkaido Prefecture, alt. 340 m (3)	60	2x	1779 ^b , 1784, 1786 ^b
Asarigawa-onsen, Otaru, Hokkaido Prefecture, alt. 170 m (1)	60	2x	1113
Touma-syonyudo, Touma-cho, Hokkaido Prefecture, alt. 240 m (1)	118	4x	1787 ^b
Owani-onsen, Owani-machi, Aomori Prefecture, alt. 300 m (1)	60	2x	2459
Tyuson-ji, Hiraizumi-cho, Iwate Prefecture, alt. 90 m (1)	60	2x	1896
Sakunami, Sendai, Miyagi Prefecture, alt. 310 m (1)	60	2x	2441
Kawasaki-machi, Shibata-gun, Miyagi Prefecture, alt. 820 m (1)	60	2x	1660
Houhara-machi, Yamagata, Yamagata Prefecture, alt. 470 m (1)	60	2x	2020
Haguro-san, Higashitagawa-gun, Yamagata Prefecture, alt. 150 m (3)	60	2x	2133, 2134, 2138
Atsushiokanou-mura, Fukushima Prefecture, alt. unknown (2)	60	2x	1486, 1555
Iwatsuki-machi, Kitakata, Fukushima Prefecture, alt. 650 m (2)	60	2x	1558, 1592
Yanaizu, Kawanuma-gun, Fukushima Prefecture, alt. 220 m (1)	60	2x	2278 ^b
Awano-machi, Kamitsuga-gun, Tochigi Prefecture, alt. 300 m (1)	60	2x	1063
Doai, Minakami-machi, Tone-gun, Gunma Prefecture, alt. 700 m (1)	60	2x	1724
Mitsuishi-yama, Kimitsu, Chiba Prefecture, alt. 200 m (1)	60	2x	1553 ^b
Mt. Mutsuishi, Okutama-machi, Tokyo Prefecture, alt. 1400 m (1)	60	2x	1566
Inoue, Hanno, Saitama Prefecture, alt. 180 m (1)	60	2x	2470
Yakeyama, Tsukui-machi, Kanagawa Prefecture, alt. 1020 m (1)	60	2x	1653
Sasanodaira, Hakushu-machi, Yamanashi Prefecture, alt. 1500 m (1)	60	2x	1600 ^b
Hirogawara, Ashiyasu-mura, Yamanashi Prefecture, alt. 1550 m (2)	118	4x	1665 ^b , 1666
Kamosawa, Tabayama-mura, Yamanashi Prefecture, alt. 580 m (1)	60	2x	1580
Aoki-kosen, Nirasaki, Yamanashi Prefecture, alt. 1140 m (2)	60	2x	1550, 1551
Iwadono, Otsuki, Yamanashi Prefecture, alt. 390 m (1)	60	2x	1552
Aikawa-machi, Sado-gun, Niigata Prefecture, alt. 180 m (1)	60	2x	1986
Niibo-mura, Sado-gun, Niigata Prefecture, alt. 100 m (1)	60	2x	1984
Ogi-machi, Sado-gun, Niigata Prefecture, alt. 20 m (1)	60	2x	1987
Zenzan-ji, Ueda, Nagano Prefecture, alt. 580 m (1)	60	2x	2150 ^b
Shiokawa, Oshika-mura, Nagano Prefecture, alt. 1360 m (1)	60	2x	1825
Norikura-kogen, Azumi-mura, Nagano Prefecture, alt. 1480 m (1)	120	4x	1709
Oshika-mura, Nagano Prefecture, alt. 1750m, 1800 m (2)	120	4x	1472, 1473
Taira-mura, Higashitonami-gun, Toyama Prefecture, alt. 330 m (2)	60	2x	1955 ^b , 1956
Kandadani, Wajima, Ishikawa Prefecture, alt. 110m, 170 m (2)	60	2x	1920 ^b , 1923 ^b
Kakuma-machi, Kanazawa, Ishikawa Prefecture, alt. 160 m (3)	60	2x	1935 ^b , 1936, 1937
Yugiri-toge, Kanazawa, Ishikawa Prefecture, alt. 800 m (1)	60	2x	1554
Eiheiji, Eiheiji-cho, Yoshida-gun, Fukui Prefecture, alt. 300 m (1)	60	2x	1907
Akame-machi, Nabari, Mie Prefecture, alt. 300 m (1)	60	2x	2429
Shirakawago, Shirakawa-mura, Gifu Prefecture, alt. 520 m (2)	60	2x	1959, 1960 ^b
Murou-mura, Uda-gun, Nara Prefecture, alt. 360 m (1)	60	2x	2425
Koya-san, Ito-gun, Wakayama Prefecture, alt. 790 m (1)	60	2x	2317
Nishinoshima, Oki-gun, Shimane Prefecture, alt. unknown (1)	60	2x	1669 ^b
Amedaki, Kokufu-cho, Iwami-gun, Tottori Prefecture, alt. 300 m (1)	60	2x	2465
Katsuura, Kotomami-cho, Kagawa Prefecture, alt. 300 m (2)	60	2x	2281 ^b , 2283
Kaminanokawa, Agawa-mura, Kochi Prefecture, alt. 800 m (1)	60	2x	2316 ^b
EASTERN NORTH AMERICA			
Leverett Pond, Massachusetts, U.S.A., alt. unknown (2)	58	2x	1313, 1492
Jericho, Chittenden Co., Vermont, U.S.A., alt. 340 m (2)	58	2x	1823, 1824
Mt. Albert, Gaspé Peninsula, Canada, alt. unknown (1)	87	3x	1670

a: Specimen number of N. Nakato. b: Specimen examined for spore length.

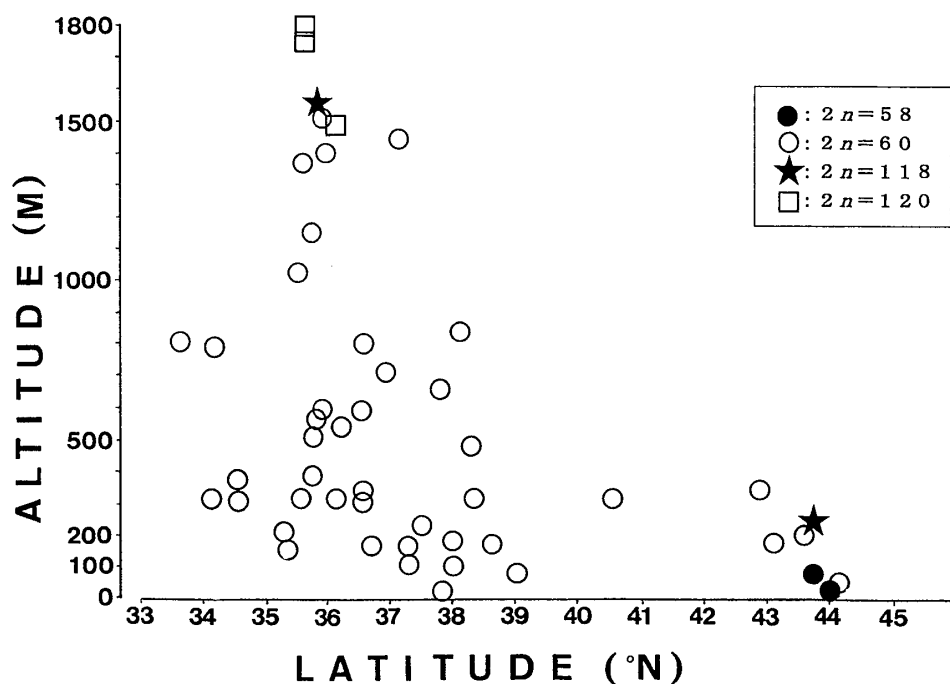


FIG. 4. Altitudinal and latitudinal distribution of four cytotypes of the *Adiantum pedatum* complex in Japan. Materials in Tables 1 and 2, except for those whose altitudes are unknown, are cited.

includes the variation of other three cytotypes completely (Fig. 5).

Spore size in the North American *Adiantum pedatum* sensu stricto ($2x$) was 34–40 μm , 37–47 μm in *A. aleuticum* ($2x$) and 45–58 μm in *A. viridimontanum* ($4x$). The spores of the tetraploid *A. viridimontanum* are therefore larger than the spores in the diploid species (Paris 1993). In contrast, no clear differences exist among the Japanese cytotypes; the mean (\pm SD) was $40.2 \pm 2.3 \mu\text{m}$ in the $2n = 58$ diploids ($N = 60$), $43.5 \pm 3.5 \mu\text{m}$ in the $2n = 60$ diploids ($N = 320$), $45.0 \pm 2.8 \mu\text{m}$ in the $2n = 118$ tetraploids ($N = 40$). Mature spores in the $2n = 120$ cytotypes were unavailable and could not be determined.

Cytogeography

The genus *Adiantum* has the same base numbers, $x = 29$ and $x = 30$, as the *A. pedatum* complex (Lovis 1977, Walker 1984). Which base number is ances-

tral for *Adiantum*? Tryon & Tryon (1982) argued that $n = 30$ is more frequent than $n = 29$ in the genus, and the base number $x = 29$ in several species is a second series of chromosome numbers. We reviewed all previous chromosome counts of *Adiantum*. Of the 150–200 species in the genus (Copeland 1947, Lin 1990, Tryon 1990), chromosome numbers have been reported for 67 species (or species complexes). Forty two species (63%) have $x = 30$, eight (12%) have $x = 29$, eight (12%) have both $x = 29$ and 30, three (4%) show only aneuploidy, and the counts for the remaining six (9%) are only approximate (Chiarugi 1960, Fabbri 1963, 1965, Löve *et al.* 1977, Goldblatt 1981, 1984, 1985, 1988, Walker 1984, Goldblatt & Johnson 1990, 1991, 1994, 1996, 1998, 2000, 2003, Takamiya 1996). Thus the base number $x = 30$ is predominant in the genus.

A recent molecular phylogeny revealed that *Adiantum* (Pteridaceae, Adiantoidae) and

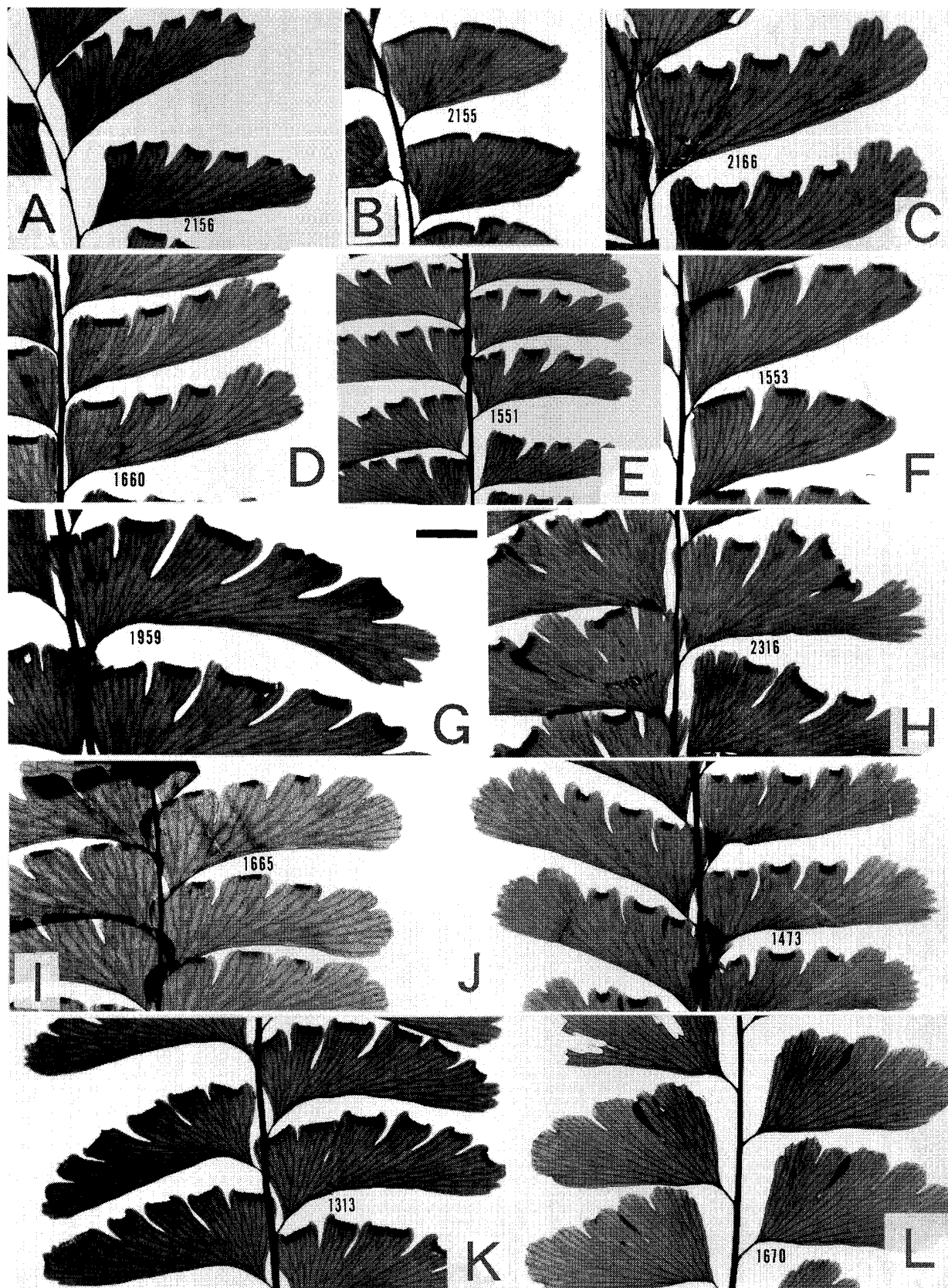


FIG. 5. Fertile (A-K) and sterile (L) pinnules of some voucher specimens. A-C. Japanese $2n = 58$ diploid. A. no. 2156. B. no. 2155. C. no. 2166. D-H. Japanese $2n = 60$ diploid. D. no. 1660. E. no. 1551. F. no. 1553. G. no. 1959. H. no. 2316. I. Japanese $2n = 118$ tetraploid, no. 1665. J. Japanese $2n = 120$ tetraploid, no. 1473. K. North American $2n = 58$ diploid, no. 1313. L. North American $2n = 87$ triploid, no. 1670. Scale bar = 5 mm.

Vittariaceae (including *Vittaria*, *Antrophyum*, *Polytaenium* and *Ananthacorus*) form a monophyletic group, which is successively sister to Pteridaceae (including *Taenitis*, *Platyzoma*, *Pteris*, *Onychium*, *Bommeria*, *Notholaena*, *Hemionitis*, *Doryopteris*, *Cheilanthes*, *Pellaea* and *Argyroschisma*) and to *Coniogramme* (Pteridaceae, *Cheilanthes* in all ML, MP and NJ trees (Hasebe *et al.* 1995). Other phylogenies also showed that *Adiantum* and allied genera are rooted by *Coniogramme* (Crane *et al.* 1995, Schneider *et al.* 2004). As to base chromosome number, Vittariaceae have $x = 30$. Pteridaceae have $x = 29$ and 30 with some exceptions, apparently derived from aneuploidy (*Taenitis*, $x = 22$ and *Platyzoma*, $x = 38$), and *Coniogramme* has $x = 30$ consistently (Lovis 1977, Walker 1987). These data strongly imply that the ancestral base number in Pteridaceae is $x = 30$, from which $x = 29$ and other aneuploid numbers diverged. It is likely the same in the *A. pedatum* complex.

Present and previous observations show that in the *Adiantum pedatum* complex both the assumed ancestral ($x = 30$) and derived ($x = 29$) diploid cytotypes occur in eastern Asia (Japan, eastern Himalaya), whereas only the derived cytotype ($x = 29$) is in North America. The *Adiantum pedatum* complex occurs mainly in cool temperate zones and is one of the northernmost elements of the genus (Fig. 3). It is likely that during past geologic times associated with climatic changes, the *A. pedatum* complex or an *A. pedatum*-like ancestor migrated repeatedly southward and northward, resulting in changes in distribution range. Eastward and westward migration must have occurred also in changing but similar climatic zones. Transpacific floristic exchanges between eastern Asia and North America occurred via the Bering land bridge during the late Tertiary and Quaternary (Hultén 1968, Hong 1983, Kato & Iwatsuki 1983, Wen 1999, Tiffney & Manchester 2001, Xiang & Soltis 2001). We propose that the $x = 29$ diploid(s) originated within the $x = 30$ diploid populations in Asia, then spread to North America.

An alternative explanation is that plants with $x = 30$ became extinct in North America, leaving behind only diploids with $x = 29$. This scenario seems less likely than an eastward migration of only the $x = 29$ cytotype.

In a preliminary report based on unpublished data, Paris *et al.* (1990) described geographical and chromosomal isolating mechanisms to have been important in the divergence of the three diploid species of the *A. pedatum* complex in North America (*i.e.*, the eastern North American *A. pedatum*, the western and eastern North American *A. aleuticum*, and the Asian '*A. pedatum*'). Our results indicate that chromosomal isolation likely occurs in Asia, but not between Asia and North America.

Outside Japan, *Adiantum pedatum* occurs widely in continental Asia, from Far East Russia and Korea to China, Bhutan, Nepal, India and Pakistan (Fig. 3). No chromosomal data are available for this large area except for a single chromosome count of $n = 29$ from Sikkim (Verma in Mehra 1961). To understand better the systematics and biogeography of the whole *A. pedatum* complex and in particular to test the proposed eastward migration, extensive comparative morphological, molecular phylogenetic, and phylogeographic analyses are needed.

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